

# Estimating the risk of Amazonian forest dieback

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## Summary

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- Climate change will very likely affect most forests in Amazonia during the course of the 21st century, but the direction and intensity of the change are uncertain, in part because of differences in rainfall projections. In order to constrain this uncertainty, we estimate the probability for biomass change in Amazonia on the basis of rainfall projections that are weighted by climate model performance for current conditions.
- We estimate the risk of forest dieback by using weighted rainfall projections from 24 general circulation models (GCMs) to create probability density functions (PDFs) for future forest biomass changes simulated by a dynamic vegetation model (LPJmL).
- Our probabilistic assessment of biomass change suggests a likely shift towards increasing biomass compared with nonweighted results. Biomass estimates range between a gain of 6.2 and a loss of 2.7 kg carbon m<sup>-2</sup> for the Amazon region, depending on the strength of CO<sub>2</sub> fertilization.
- The uncertainty associated with the long-term effect of CO<sub>2</sub> is much larger than that associated with precipitation change. This underlines the importance of reducing uncertainties in the direct effects of CO<sub>2</sub> on tropical ecosystems.

## Introduction

Old-growth rainforests in the Amazon basin store *c.* 93 ± 23 Pg of carbon (Pg C) in their biomass (Malhi *et al.*, 2006). Annually, tropical forests process *c.* 18 Pg C through respiration and photosynthesis (Malhi & Grace, 2000). This is more than twice the present amount of fossil fuel emissions (Dirzo & Raven, 2003). Currently the Amazon rainforest appears to be a net sink for atmospheric CO<sub>2</sub>, but drought events, such as the 2005 drought, potentially affect tropical forest by changing forest structure and dynamics, which lead to loss of biomass carbon (Phillips *et al.*, 2009). The quantitative assessment of this risk is a prerequisite for the stabilization of Amazonian rainforests and is therefore of global importance for climate protection measures.

Climate projections from the current generation of general circulation models (GCMs) suggest an average increase in global temperature of *c.* 3.3°C by the end of the 21st century (IPCC, 2007), but they differ widely in their projections of rainfall because of different assumptions about the underlying mechanisms of rainfall formation (Li *et al.*, 2006). The uncertainty for changes in rainfall

regimes is therefore high. Shifts in the rainfall regime may significantly alter vegetation structure and composition in the Amazon basin (Lapola *et al.*, 2009; Malhi *et al.*, 2009). Field observations indicate that prolonged drought events may lead to increasing plant physiological stress and reduced productivity of trees (Brando *et al.*, 2008; Phillips *et al.*, 2009). Decreases in evapotranspiration and therefore convective precipitation could further accelerate drought conditions and destabilize the tropical ecosystem as a whole (Betts *et al.*, 2004). The so-called ‘Amazon forest dieback’ by the middle of the 21st century was first simulated by the Hadley Centre coupled ocean–atmosphere–vegetation model and was caused by a positive feedback from increasing atmospheric CO<sub>2</sub> concentrations, which increased warming and decreased precipitation (Cox *et al.*, 2000). This led to vegetation biomass loss in the Amazon basin, which further accelerated CO<sub>2</sub> emissions and, in turn, increased temperature and reduced precipitation (Cox *et al.*, 2004). Owing to the massive local effects of this feedback along with its system-wide repercussions, the Amazon rainforest has been identified as one potential ‘tipping element’ of the Earth system (Lenton *et al.*, 2008).

The probability for large-scale Amazon forest dieback is currently discussed in the literature. Field observations (Malhi *et al.*, 2004, 2006; Phillips *et al.*, 2009), drought manipulation experiments (Nepstad *et al.*, 2007; Brando *et al.*, 2008), remote sensing (Saleska *et al.*, 2007) and modelling studies (Cox *et al.*, 2004; Cramer *et al.*, 2004; Sitch *et al.*, 2008) have given contrasting results: field observations and experiments indicate high sensitivity of tropical forest biomass and structure to the degree of drought conceivable under the climate change projections. For example, the observed responses of rainforests to drought events such as the 1997/1998 El Niño event range from high tree mortality (*c.* 26%) in a forest with seasonal rainfall in East Kalimantan (Van Nieuwstadt & Sheil, 2005) to no mortality in Panama (Condit *et al.*, 2004) and several intermediate responses (Condit *et al.*, 1995; Kinnaird & O'Brien, 1998; Williamson *et al.*, 2000). During the 2005 drought in Amazonia, Phillips *et al.* (2009) measured greatly increased tree mortality alongside rather small declines in growth in the surviving trees. By contrast, some remote sensing studies suggest a vegetation green-up during dry periods as a result of enhanced plant productivity from increased solar radiation (Huete *et al.*, 2006; Saleska *et al.*, 2007). Modelling studies display a great variety of projections for future changes in neotropical vegetation, ranging from a potential reduction in forest cover (Cox *et al.*, 2000, 2004; Cramer *et al.*, 2004; Schaphoff *et al.*, 2006; Scholze *et al.*, 2006; Salazar *et al.*, 2007; Sitch *et al.*, 2008) to no dangerous reduction in forest cover (Walker *et al.*, 2009).

One explanation for the differences between these studies appears to be linked to the different representation of physiological processes in these models – in particular, there is considerable disagreement concerning the amount of CO<sub>2</sub>-related buffering against drought stress. Cowling & Shin (2006) have analysed the extent to which these processes are sensitive to temperature, precipitation and CO<sub>2</sub>, but were unable to identify a single key factor or threshold. Another, highly significant, part of the variability between published assessments appears to be the result of the selection of climate forcings from different projections. Since rainfall shows the highest variation between models, here we study the uncertainty in rainfall projections and how it propagates to projections of future biomass change in the Amazon region.

Implicitly, all earlier climate projections have been treated as if they were equally plausible, independent of the quality of the underlying climate model (IPCC, 2007; Malhi *et al.*, 2008, 2009). Assuming that greater agreement between model simulations and current climate implies higher model quality, Jupp *et al.* (2010) instead weighted the climate projections based on the ability of each climate model to produce key aspects of the observed climate. In their study, they derived regional probability density functions (PDFs) as weightings for the 24 IPCC-AR4

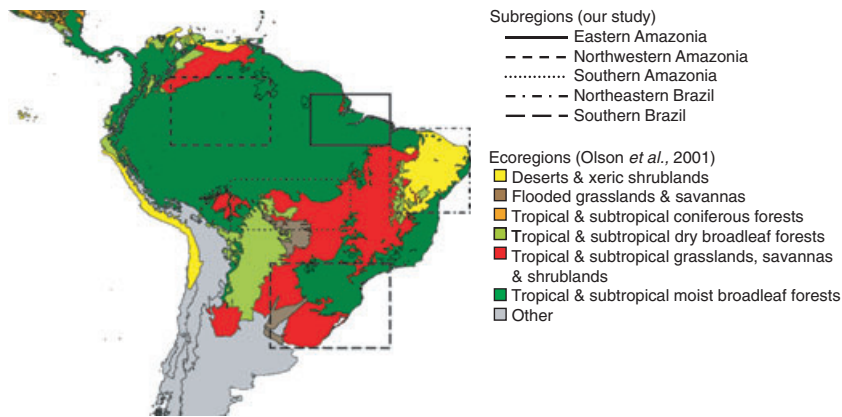
rainfall projections for Amazonia (IPCC-AR4, Intergovernmental Panel on Climate Change, Assessment Report 4). Here, we apply these weights to forest biomass simulations obtained by the Lund–Potsdam–Jena Dynamic Global Vegetation Model for managed land (LPJmL, Sitch *et al.*, 2003; Gerten *et al.*, 2004; Bondeau *et al.*, 2007) for five regions throughout South America. By emphasizing the results of simulated biomass from climate projections with higher weightings (i.e. better ability to reproduce current rainfall patterns), and de-emphasizing the results from climate projections with lower weightings, the range of estimated biomass change can be seen as being more robust. We use a probabilistic approach to separately quantify the uncertainty in ecosystem response to changes in rainfall from different climate models, as well as the uncertainty arising from different assumptions about the effects of rising atmospheric CO<sub>2</sub> concentrations on vegetation growth and water-use efficiency (CO<sub>2</sub> fertilization, e.g. Hickler *et al.*, 2008; Lapola *et al.*, 2009). Our main goals are to estimate the relative probability of dangerous biomass loss in these regions with a particular focus on Amazonia; to discuss the ecophysiological bases for responses to CO<sub>2</sub> and climate; and to evaluate the upper and lower limits of potential biomass change.

## Materials and Methods

The study is conducted for five regions covering a large area of South America and different vegetation types (Fig. 1). These regions are chosen to cover a broad range of vegetation types with different amounts of biomass. In the following, we describe the vegetation model applied in this study and the environmental drivers used in our simulations. Subsequently, we discuss the evaluation of model output in comparison to observations and the weighting of biomass responses according to the plausibility of the 24 climate projections.

### Forest biomass simulations: the generic vegetation model LPJmL

We apply the generic vegetation model LPJmL to the study region. The model originates from the Lund–Potsdam–Jena Dynamic Global Vegetation Model (LPJ, Sitch *et al.*, 2003) and was further developed with an improved water balance (Gerten *et al.*, 2004) and managed land component (Bondeau *et al.*, 2007). Like LPJ, LPJmL simulates vegetation processes for cells in a grid with mesh sizes of 0.5° in longitude and latitude. In any grid cell, the simulation is driven by an input of monthly climate (air temperature (°C), precipitation (mm), cloud cover (%), number of wet days), annual atmospheric CO<sub>2</sub> concentration and soil texture. The performance of three plant functional types (PFTs) reflecting major vegetation types in the Amazon



**Fig. 1** Map of ecoregions in northern South America according to the classification of Olson *et al.* (2001). Boxes indicate the subregions as defined for this analysis.

basin, namely tropical broadleaved evergreen trees, tropical broadleaved raingreen trees and  $C_4$ -nonwoody vegetation, is described by physiological processes. PFTs can be conceived as plant species grouped by specific attributes controlling their physiology and dynamics. The vegetation in each grid cell is represented as a mixture of these three PFTs, where each PFT covers a dynamic proportion of the modelled area. Physiological processes (e.g. photosynthesis, plant respiration and microbial decomposition) and associated fluxes of carbon and water between soil layers, vegetation and the atmosphere are simulated with a daily time step, for which monthly values of climate are interpolated to quasi-daily values. Daily precipitation is distributed by a weather generator according to total monthly precipitation and the number of wet days (Gerten *et al.*, 2004). A modified Farquhar photosynthesis model (Farquhar *et al.*, 1980) generalized for global modelling purposes from Collatz *et al.* (1991) calculates canopy photosynthesis and thus gross primary productivity (GPP) as a function of absorbed photosynthetically active radiation, temperature and leaf intercellular  $CO_2$  concentration under the assumption of optimal nitrogen availability. The leaf intercellular  $CO_2$  concentration depends on the ambient atmospheric  $CO_2$  concentration and stomatal conductance. Stomatal conductance is determined by the atmospheric demand, which is calculated from leaf conductance under nonwater-stressed photosynthesis rates and water supply, which depends on plant root-weighted soil moisture availability and maximum sap flow rates. If the atmospheric demand is higher than the water supply, canopy conductance is reduced until transpiration equals the supply, which results in lower photosynthesis rates as a result of reduced diffusion of  $CO_2$  into the leaves. Net primary productivity (NPP) is the difference between GPP and the  $CO_2$  released from growth and maintenance respiration, which results in the daily assimilated carbon. NPP is allocated annually to the different carbon compartments of the plant, such as leaves, sapwood and fine roots, according to specified allometric constraints (detailed model descriptions are given in Sitch *et al.*, 2003). LPJ and

LPJmL have been evaluated against many types of observations, on the global (Gerten *et al.*, 2004) and regional scale for boreal forests (Lucht *et al.*, 2002), the African Sahel (Hickler *et al.*, 2005) and tropical ecosystems (Cramer *et al.*, 2004; Cowling & Shin, 2006; Poulter *et al.*, 2009).

For our study, we apply LPJmL in its natural vegetation mode to concentrate on climate risks and  $CO_2$  fertilization effects on the future stability of the Amazon rainforest *per se*, as detailed process understanding is still lacking. The relative importance of climate vs land use change for Amazon rainforests has been addressed in Poulter *et al.* (2009). The forest response is expressed by the change in the vegetation carbon storage or 'biomass' (in  $kg\ C\ m^{-2}$ ).

### Climate model projections

We use climate projections from those coupled general circulation models (CGCMs) that have been used to assess the coupled atmosphere–ocean dynamics for the Coupled Model Intercomparison Project 3 (CMIP3) carried out for the IPCC's *Fourth Assessment Report* (IPCC-AR4, IPCC 2007). These data comprise the output from 24 climate models (available at <https://esg.llnl.gov:8443/>). Here, we use results from the A1B-SRES emission scenario alone, which assumes a future world of rapid economic growth (SRES, IPCC special report on emission scenarios, Nakicenovic *et al.* 2000). Global population starts to decline by mid-century accompanied by the introduction of new and more efficient technologies. Atmospheric  $CO_2$  concentrations increase to 717 ppm by the year 2100 (Nakicenovic *et al.*, 2000).

### Removing climate model bias

All current climate model simulations exhibit considerable biases for the study region. We therefore applied an anomaly approach in order to remove climate model bias and also to standardize the climate input for LPJmL. For each month and each grid cell, the climate model bias for the reference

period (1961–1990) is determined as the difference (for temperature) between or the ratio (for precipitation and cloud cover) of the 30 yr means of climate model output and observed climate data assuming constant bias for future climatic conditions. Climate data are taken from a homogenized and extended CRU TS2.1 global climate data set (Österle *et al.*, 2003; Mitchell & Jones, 2005).

### Study design

The Lund–Potsdam–Jena Dynamic Global Vegetation Model for managed land is run for the 24 IPCC-AR4 climate projections on a 0.5° resolution longitude/latitude grid for the five regions as shown in Fig. 1. Pre-industrial conditions in carbon pools and vegetation distribution are estimated by running the model through a 1030 yr spin-up period, where the first 1000 yr are simulated with a repeated CRU climate data cycle from 1901 to 1930 under pre-industrial atmospheric CO<sub>2</sub> concentrations, and the remaining 30 yr are simulated with climate model-specific spin-up to allow adjustment of vegetation to variations in interannual variability between the models. Transient runs with anomaly-corrected climate model data are conducted from 1901 to 2100.

The standard A1B-SRES emission trajectory assumes increases in CO<sub>2</sub> from 369.5 ppm in the year 2000 to 717 ppm in the year 2100. To evaluate the effects of CO<sub>2</sub> fertilization, we conducted two simulation experiments: standard CO<sub>2</sub> fertilization effects in addition to climate change, including a reduced transpiration rate and higher amount of photosynthesis ('CLIM + CO<sub>2</sub>' scenario); and no additional CO<sub>2</sub> fertilization effects compared with current conditions ('CLIM-only' scenario).

### Evaluation of current biomass simulations

For the evaluation of simulated biomass under current conditions, the average modelled biomass of 1970–2000 for each of the five regions is compared with available data from a combined approach of plot and satellite measurements from Saatchi *et al.* (2007) and from plot measurements (Houghton *et al.*, 2001; Baker *et al.*, 2004; Malhi *et al.*, 2006). The map from Saatchi *et al.* (2007) is available at a spatial resolution of 1 km and is aggregated to a spatial resolution of 0.5° × 0.5° for comparison with simulated data. For the comparison of simulated biomass with plot measurements, all plots within one region are averaged (Table S2).

### Application of climate model weightings and estimation of PDFs for biomass

Jupp *et al.* (2010) weighted the 24 IPCC-AR4 climate projections according to their ability to reproduce current observed patterns of rainfall (mean and interannual

variability) in each of the five regions using a Bayesian approach. The study of Jupp *et al.* (2010) and our study focus on rainfall, because it is (along with temperature, with which it is correlated) a driving variable for which future projections are highly uncertain. Changes in precipitation may cause substantial changes in biomass and it is therefore crucial to quantify the uncertainty in the projections. To weight the climate model projections, Jupp *et al.* (2010) initially assigned a uniform prior probability  $\pi(m_i)$  to the 24 climate projections  $m_i$ , with  $i$  being model 1–24 (see list of model names in Supporting Information, Table S1). The posterior (or weighted) PDFs for the rainfall projections  $p(m_i)$  were then calculated from the prior PDF and the observed data  $d$  by two successive applications of Bayes' formula

$$p(m_i) \propto f(d|m_i)\pi(m_i) \quad \text{Eqn 1}$$

The first application of Bayes' formula takes account of each projection's ability to reproduce observed mean rainfall, while the second assesses the ability of the projections to fit the observed interannual variability following correction for any bias in mean rainfall. The weights for one region are determined independently of the weights for another region. No information from other climate variables (e.g. temperature) is used, as they would show correlation to the rainfall data and hence lead to double-counting of data in the weighting procedure. The procedure is described in detail in Jupp *et al.* (2010). The posterior rainfall PDFs calculated by Jupp *et al.* (2010) are used in our study to estimate the weighted cumulative distribution functions (CDFs) and PDFs for future biomass change.

The biomass change  $b_i$  associated with model  $i$  for each region is calculated as the difference between the simulated biomass averaged over 2070–2100 and the simulated biomass averaged over 1970–2000. We then calculate the unweighted biomass CDFs,  $cp(x)$ :

$$cp(x) = \frac{1}{n} N(b_i \leq x) \quad \text{Eqn 2}$$

where  $x$  denotes the range of possible biomass changes and  $N$  is the number of values fulfilling the condition  $b_i \leq x$ . The weighted biomass CDFs are then calculated as

$$cp(x) = \frac{1}{n} N(b_i p(m_i) \leq x) \quad \text{Eqn 3}$$

using the probabilities  $p(m_i)$  from Jupp *et al.* (2010).

To obtain the unweighted and weighted biomass PDFs, a uniform sample of 10 000 values was drawn from the unweighted and weighted CDFs and a smooth density function was fitted (R Development Core Team 2008).

## Evaluation of future biomass changes

We identify the most likely ranges of biomass change as the maximum value of the PDFs (modal value) and the corresponding interquartile range. These values are good indicators for the shift in biomass change projections (modal value) and the underlying uncertainty of predictions (interquartile range). In the results section, the modal value and its interquartile range are denoted as 'most likely range'. The overall range of potential biomass change is reflected by the 5% and 95% quantiles of the combined distribution of the two weighted scenarios with and without the physiological effects of CO<sub>2</sub>. In the Results section, we refer to this range as 'overall range'.

We additionally determine the probability for 'biomass loss' both including and excluding CO<sub>2</sub> fertilization, where 'biomass loss' is defined as any negative biomass change. We also determine the probability for 'dieback', for which we define as an arbitrary limit a biomass loss of at least 25% of the total biomass in 2070–2100 in comparison to 1970–2000.

## Results

Climatic conditions and therefore the amount of present and projected biomass changes vary strongly between the five regions and among climate projections (see Table S1). Overall, the simulated current biomass (1970–2000) agrees well with observed values (Table 1). Generally, Bayesian weighting indicates a lower probability of biomass loss when climate projections are not weighted (compare dashed with solid lines in Figs 2–4). When assuming strong positive effects of CO<sub>2</sub> fertilization (CLIM + CO<sub>2</sub> scenario), biomass is likely to increase across all regions. Removing CO<sub>2</sub> fertilization effects generally leads to projections of

reduced biomass by the end of the century with a wide range of magnitudes. The uncertainty associated with precipitation change is much lower than that associated with the long-term effect of CO<sub>2</sub>. Region-specific results are described in more detail in the following sections.

### Eastern Amazonia

The simulated biomass under current climatic conditions is on average 9.1 kg C m<sup>-2</sup> and ranges from 6.3 to 13.0 kg C m<sup>-2</sup> within the region (Table 1, region range) and from 3.5 to 14.4 kg C m<sup>-2</sup> across all IPCC-AR4 projections (Table 1, model range). The simulated biomass lies in the range of the measurements, which are on average 9.6 and 15.7 kg C m<sup>-2</sup> (Table 1).

Biomass always decreases when CO<sub>2</sub> effects are not taken into account (CLIM only), while increases are projected with strong CO<sub>2</sub> effects (CLIM + CO<sub>2</sub>, see Fig. 2a,b and Table 2). The overall range of the weighted scenarios has a large uncertainty and spans biomass projections from -5.0 to 6.4 kg C m<sup>-2</sup> (Table 2). The most likely range of biomass change is narrower; that is, the uncertainty of model predictions is reduced by model weighting. The modal values in eastern Amazonia are 6.2 and -0.9 kg C m<sup>-2</sup> for the CLIM + CO<sub>2</sub> and the CLIM-only experiments, respectively (Fig. 2b, grey shaded areas, and Table 2). Weighting the biomass projections leads to a relative increase in the projected biomass compared with nonweighted results (median value of -0.9 vs -3.0 kg C m<sup>-2</sup> for the CLIM-only scenario and 2.1 vs 4.9 kg C m<sup>-2</sup> for the CLIM + CO<sub>2</sub> scenario, Fig. 2a, Table 2); that is, climate models producing more favourable conditions for forests obtained slightly higher weightings than those with unfavourable conditions. The probabilities of any biomass loss (negative biomass change) are 0.15 and 86.4% with and

**Table 1** Comparison of simulated and observed biomass in the five regions of South America

Region	Biomass (kg C m <sup>-2</sup> )				
	Simulated <sup>a</sup>			Observed	
	Model range <sup>b</sup>	Region range <sup>c</sup>	Mean <sup>d</sup>	Remote sensing and plots <sup>e</sup>	Measurements <sup>f</sup>
Eastern Amazonia	3.5–14.4	6.3–13.0	9.1	0.6–16.2 (9.6)	15.7
Northwestern Amazonia	7.8–19.7	6.7–20.0	15.0	0.6–18.4 (12.0)	16.9
Southern Amazonia	6.3–11.9	7.2–12.0	9.2	0.6–14.1 (4.4)	11.2
Northeastern Brazil	2.6–8.4	0.3–17.2	6.1	0.6–9.8 (1.4)	–
Southern Brazil	6.5–12.2	3.0–20.4	10.4	–	–

<sup>a</sup>Vegetation carbon as simulated from the Lund–Potsdam–Jena Dynamic Global Vegetation Model for managed land (LPJmL).

<sup>b</sup>The model range gives the range of mean biomass across the region for the 24 climate projections.

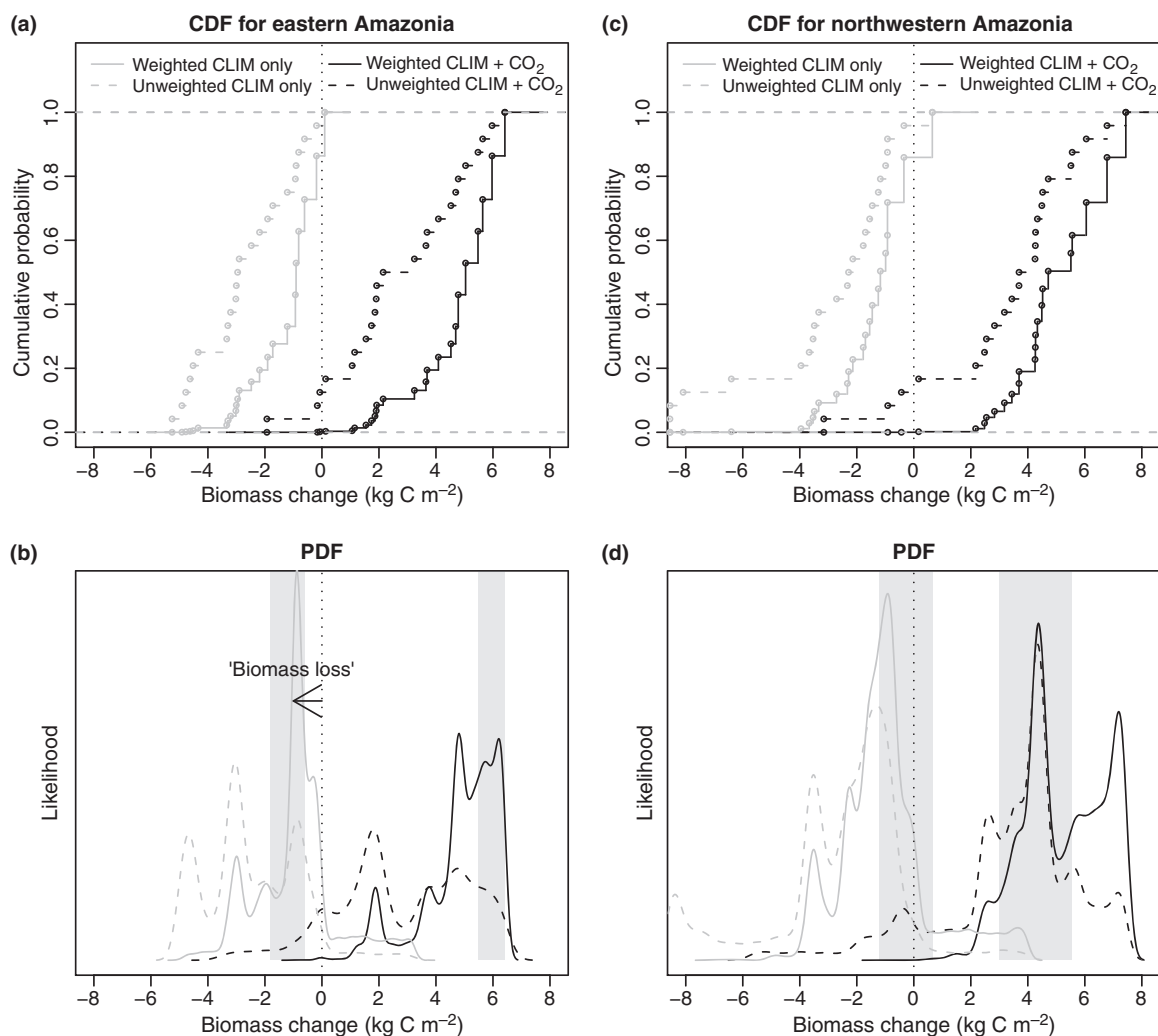
<sup>c</sup>The region range gives the range of mean biomass across the 24 climate projections for the particular region.

<sup>d</sup>The mean gives the mean biomass over all models and grid cells.

<sup>e</sup>From Saatchi *et al.* (2007): given is the minimum and maximum (mean) values of above-ground living biomass (AGLB). The amount of biomass was averaged for each region. AGLB was converted to vegetation carbon by dividing the original numbers by 2 (Larcher, 2001).

<sup>f</sup>Measurement values from Houghton *et al.* (2001), Baker *et al.* (2004) and Malhi *et al.* (2006) were averaged for all plots within each region.

For details see Supporting Information, Table S2.



**Fig. 2** Cumulative distribution functions (CDFs) and probability density functions (PDFs) for biomass changes in eastern and northwestern Amazonia for 2070–2100 vs 1970–2000. (a, c) The CDFs provide the numerical probabilities associated with biomass change. The dotted vertical lines denote the zero line (points to the left of this line always denote ‘biomass loss’). Note that the weighting changes the probabilities of biomass change in the CDF. When resampled, this propagates through to give PDFs for biomass change, which are pushed to the right (made more positive). (b, d) The maximum (modal) values of the PDFs (with interquartile range, shaded grey areas) display the ‘most likely’ biomass change as defined in the Materials and Methods section. Black lines, biomass changes assuming the effects of CO<sub>2</sub> fertilization (CLIM + CO<sub>2</sub>); grey lines, biomass changes assuming no CO<sub>2</sub> effects (CLIM only). The dashed lines show the unweighted probabilities, the solid lines the weighted probabilities (based on the rainfall weights determined by Jupp *et al.*, 2010).

without CO<sub>2</sub> fertilization effects, respectively, and for dieback (biomass loss of > 25% of the total biomass) the probabilities are 0.0 and 15.7% (Table 3, Fig. 2a).

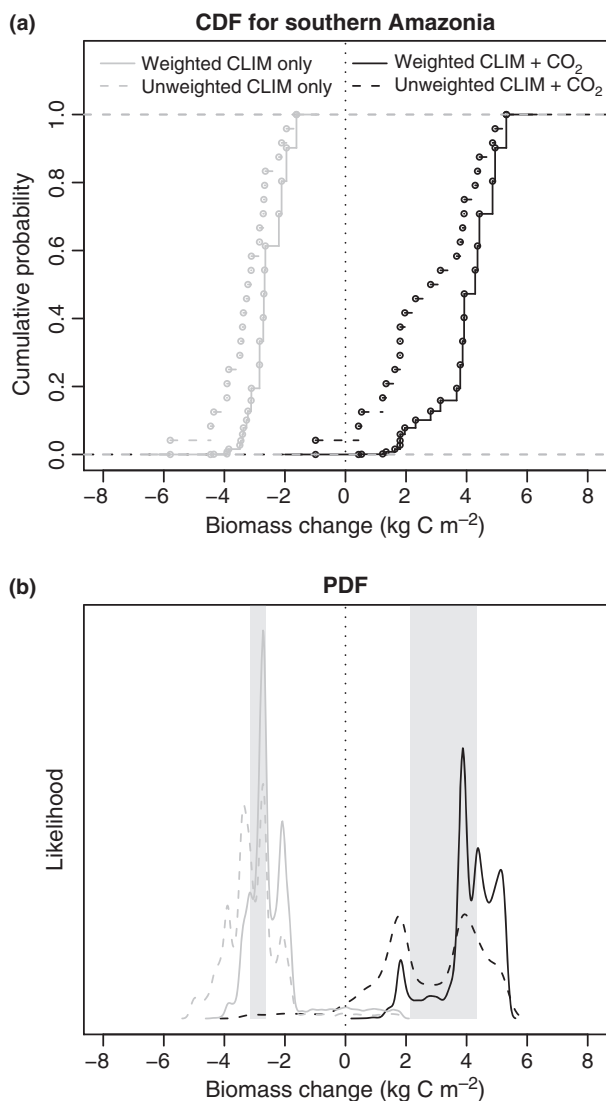
### Northwestern Amazonia

Northwestern Amazonia has the highest amounts of biomass with, on average, 12–16.9 kg C m<sup>-2</sup> (measurements, Table 1). Simulated biomass ranges in northwestern Amazonia between 6.7 and 20.0 kg C m<sup>-2</sup> and corresponds well with measurements (Table 1). Biomass changes under future climate conditions display similar patterns to eastern Amazonia. The overall change in projected biomass ranges

between -8.0 and +7.6 kg C m<sup>-2</sup> (Table 2, Fig. 2c,d). Most likely changes in biomass are at the two pronounced modal values of 4.4 and -0.9 kg C m<sup>-2</sup> for the CLIM + CO<sub>2</sub> and the CLIM-only experiments, respectively (Fig. 2d, grey shaded areas, and Table 2). The probabilities of any biomass loss are 85.9 and 0%, in the CLIM-only and CLIM + CO<sub>2</sub> scenarios, respectively, while the probabilities for dieback are 1.1 and 0%, respectively (Table 3, Fig. 2c).

### Southern Amazonia

Forests in the southern Amazonian region contain *c.* 4.4–11.2 kg C m<sup>-2</sup> (measurements, Table 1). Our simulations



**Fig. 3** Cumulative distribution functions (CDFs) (a) and probability density functions (PDFs) (b) for biomass changes in southern Amazonia for 2070–2100 vs 1970–2000. (a) The CDFs provide the numerical probabilities associated with biomass change. The dotted vertical lines denote the zero line (points to the left of this line always denote 'biomass loss'). Note that the weighting changes the probabilities of biomass change in the CDF. When resampled, this propagates through to give PDFs for biomass change, which are pushed to the right (made more positive). (b) The maximum (modal) values of the PDFs (with interquartile range, shaded grey areas) display the 'most likely' biomass change as defined in the Materials and Methods section. Black lines, biomass changes assuming the effects of CO<sub>2</sub> fertilization (CLIM + CO<sub>2</sub>); grey lines, biomass changes assuming no CO<sub>2</sub> effects (CLIM only). The dashed lines show the unweighted probabilities, the solid lines the weighted probabilities.

show a biomass range of 7.2–12.0 kg C m<sup>-2</sup> in the region, which corresponds to the measured biomass values. Based on the weighting approach, the modal values of the PDFs lie at 3.9 kg C m<sup>-2</sup> for the CLIM + CO<sub>2</sub> scenario and at -2.7 kg C m<sup>-2</sup> for the CLIM-only scenario (Fig. 3b,

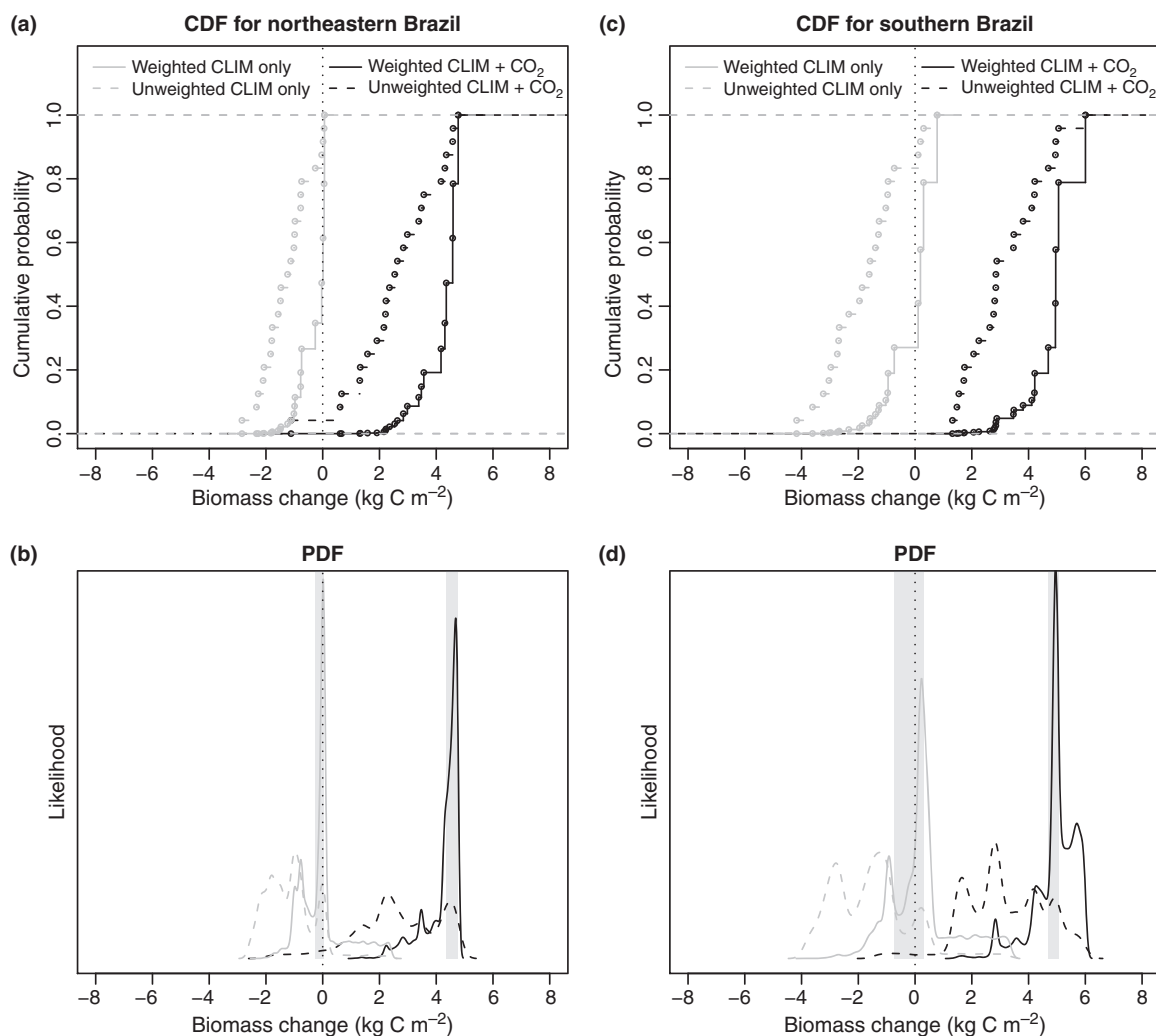
Table 2). Both peaks are close to the median value of weighted biomass change, which shifts from 4.0 to 2.8 and -3.2 to -2.7 kg C m<sup>-2</sup> in the CLIM + CO<sub>2</sub> and the CLIM-only experiments, respectively (Table 2). The probabilities of any biomass loss and dieback are high in the CLIM-only scenario (100 and 61%, respectively), but low in the CLIM + CO<sub>2</sub> scenario (Table 3, Fig. 3a,b).

### Northeastern and southern Brazil

For the northeastern part of Brazil, the modelled biomass is on average 6.1 kg C m<sup>-2</sup> and is thus at the upper end of the available measurement data (0.6–9.8 kg C m<sup>-2</sup>; Table 1). Biomass in southern Brazil is estimated to be 10.4 kg C m<sup>-2</sup>; here we are unfortunately not aware of comparable measurement data. Estimated future biomass changes (90% of the combined distributions of CLIM + CO<sub>2</sub> and CLIM-only) range from -2.1 to +4.7 kg C m<sup>-2</sup> in northeastern Brazil and -3.5 to +6.0 kg C m<sup>-2</sup> in southern Brazil (Table 2, Fig. 4b,d). Bayesian weighting leads to biomass increases in both regions. The modal values of the weighted PDFs at 4.7 and 0.01 C m<sup>-2</sup> in the northeast and 4.9 and 0.2 kg C m<sup>-2</sup> in the south indicate an increase in biomass in both the CLIM+CO<sub>2</sub> and CLIM runs once the Bayesian weighting is applied (Table 2). The probability of any biomass loss is between 0 and 47.3% in northeastern Brazil and 0 and 27% in southern Brazil for the CLIM + CO<sub>2</sub> and CLIM-only experiments, respectively. The probability of dieback lies between 0 and 1% for both regions (Table 3, Fig. 4a,c).

### Discussion

Rainfall is a direct driver of vegetation dynamics in the Amazon region and throughout Brazil. Thus, assessing future rainfall conditions is a crucial step for estimating the risks of future Amazon forest dieback. Evaluating the quality of regional projections as simulated in GCMs is difficult because of the complex nature of these models and the underlying processes and circulations. Therefore, evaluating the ability of these models to reproduce currently observed precipitation serves as a proxy that can be used to weight different GCM projections of future rainfall (Jupp *et al.*, 2010). Future biomass projections vary strongly with the projected climate as shown in the present study (Table S1). The Bayesian biomass weightings give a more differentiated picture of likely biomass changes in comparison with studies that treat potential changes with the same probability (Malhi *et al.*, 2008, 2009; Lapola *et al.*, 2009). Our results show that under the assumption of strong CO<sub>2</sub> effects, biomass increases are more likely in all five regions of Brazil. However, if CO<sub>2</sub> effects are weak, biomass reductions become much more likely. In the following, we discuss the limitations of our study approach, the ecophysiological



**Fig. 4** Cumulative distribution functions (CDFs) (a, c) and probability density functions (PDFs) (b, d) for biomass changes in northeastern and southern Brazil for 2070–2100 vs 1970–2000. (a, c) The CDFs provide the numerical probabilities associated with biomass change. The dotted vertical lines denote the zero line (points to the left of this line always denote 'biomass loss'). Note that the weighting changes the probabilities of biomass change in the CDF. When resampled, this propagates through to give PDFs for biomass change, which are pushed to the right (made more positive). (b, d) The maximum (modal) values of the PDFs (with interquartile range, shaded grey areas) display the 'most likely' biomass change as defined in the Materials and Methods section. Black lines, biomass changes assuming the effects of CO<sub>2</sub> fertilization (CLIM + CO<sub>2</sub>); grey lines, biomass changes assuming no CO<sub>2</sub> effects (CLIM only). The dashed lines show the unweighted probabilities, the solid lines the weighted probabilities.

bases of biomass responses to CO<sub>2</sub> and climate, and the range of biomass change in the five regions of northern South America.

#### Limitations of the study approach

The presented probabilities for biomass change are based on rainfall weightings described by Jupp *et al.* (2010). Higher weightings imply the assumption that climate models that are better able to reproduce the mean and variability of the current rainfall also produce more reliable projections of future rainfall. Future dynamics, however, may be related to processes not important for present climate. As discussed

by Jupp *et al.* (2010), the highest ranked models differ between the five regions, which shows that it is currently not possible to determine one climate model that describes the underlying processes of rainfall patterns in South America.

In our study, we applied the weightings from Jupp *et al.* (2010) to estimate the probability of dangerous amounts of biomass loss. A further step would be to create such biomass weightings directly by evaluating the ability of different vegetation–climate model combinations to reproduce current vegetation patterns. In this way the likelihoods of different representations of direct CO<sub>2</sub> effects could also be estimated. In the present study, we approached



**Table 2** Potential biomass changes

	Overall range of biomass change	Modal value and most likely range of biomass change		Median value of biomass change			
				CLIM + CO <sub>2</sub>		CLIM only	
		CLIM + CO <sub>2</sub>	CLIM only	u	w	u	w
	w	w	w	u	w	u	w
Eastern Amazonia	-5.0-6.4	6.2 (5.5- 6.4)	-0.9 (-1.8 to -0.6)	2.1	4.9	-3.0	-0.9
Northwestern Amazonia	-8.0-7.6	4.4 (2.9-5.5)	-0.9 (-1.2 to 0.6)	3.7	4.9	-2.3	-1.1
Southern Amazonia	-4.7-5.3	3.9 (2.1- 4.3)	-2.7 (-3.3 to -2.6)	2.8	4.0	-3.2	-2.7
Northeastern Brazil	-2.1-4.7	4.7 (4.3- 4.8)	0.01 (-0.3 to 0.05)	2.5	4.4	-1.2	0.0
Southern Brazil	-3.5-6.0	4.9 (4.7- 5.0)	0.2 (-0.7 to 0.3)	2.8	5.0	-1.6	0.1

CLIM + CO<sub>2</sub>, standard CO<sub>2</sub> fertilization effects in addition to climate change, including a reduced transpiration rate and higher amount of photosynthesis; CLIM only, no additional CO<sub>2</sub> fertilization effects compared with current conditions; w, weighted scenarios; u, unweighted scenarios. All values are shown in kg C m<sup>-2</sup>.

Overall range of biomass change given as the 5-95% quantile of the weighted CLIM + CO<sub>2</sub> and CLIM only scenarios. The most likely range of biomass is denoted as the maximum (modal) value of the weighted probability density functions (PDFs) and the interquartile range. The median value (50% probability) of the projected biomass changes for the unweighted and weighted 'CLIM + CO<sub>2</sub>' and 'CLIM only' scenario as derived from the cumulative probability functions.

**Table 3** Probability of any biomass loss and biomass loss of 25% of the total biomass as listed in Table 1

	Probability of any biomass loss (biomass change < 0 kg C m <sup>-2</sup> )		Probability of biomass loss of 25% or more	
			CLIM + CO <sub>2</sub>	
	CLIM only	CLIM + CO <sub>2</sub>	CLIM only	CLIM + CO <sub>2</sub>
Eastern Amazonia	86.40	0.15	15.70	0.00
Northwestern Amazonia	85.90	0.00	1.10	0.00
Southern Amazonia	100.00	0.00	61.30	0.00
Northeastern Brazil	47.30	0.00	1.00	0.00
Southern Brazil	27.03	0.00	0.90	0.00

CLIM + CO<sub>2</sub>, standard CO<sub>2</sub> fertilization effects in addition to climate change, including a reduced transpiration rate and higher amount of photosynthesis; CLIM only, no additional CO<sub>2</sub> fertilization effects compared with current conditions. The probabilities were derived from the biomass probability density functions (PDFs) and cumulative distribution functions (CDFs; Figs 2-4).

the uncertainty of CO<sub>2</sub> effects via two scenarios testing the range of potential responses of vegetation to CO<sub>2</sub> fertilization (i.e. strong effects vs no effects). Our study concentrates on climate change scenarios from the A1B-SRES emission scenario. Thus it is very likely that the corresponding weightings could differ under other SRES emission scenarios, but this was not the focus of the current study. Effects of climate change under different CO<sub>2</sub> emission scenarios on Amazon rainforest are published in Poulter *et al.* (2009).

Our biomass PDFs suggest that future climate in the Amazonian rainforest region is less suitable for biomass production, but that strong CO<sub>2</sub> effects could nevertheless lead to biomass increases. However, the magnitude of these

effects remains highly uncertain. Further uncertainties arise from a lack of knowledge of how the effects of increasing CO<sub>2</sub> concentrations on plants may change forest community structure as a result of the differential responses of different plant types (Granados & Körner, 2002; Phillips *et al.*, 2002; Körner, 2003), whether the positive response of CO<sub>2</sub> on plants may level off (Bazzaz, 1990) or even lead to reduction in forest carbon storage (Körner, 2004); the effects of nutrient availability (Hungate *et al.*, 2003; Chambers & Silver, 2004; Powers *et al.*, 2005); and likewise future changes in climate and vegetation associated with non-CO<sub>2</sub> emissions (Ramanathan & Feng, 2008). Accounting for these additional factors will most probably lead to a higher estimated risk of biomass loss in forest ecosystems in Amazonia.

### Ecophysiological bases for biomass responses to CO<sub>2</sub> and climate

Our results show that key uncertainties for estimating the consequences arise from the uncertain role of direct CO<sub>2</sub> fertilization in terms of enhanced photosynthetic capacity and water-use efficiency. The role of increased atmospheric CO<sub>2</sub> concentrations for photosynthesis (Norby *et al.*, 1999, 2005; Körner, 2003; Long *et al.*, 2004) and for stomatal conductance (Collatz *et al.*, 1991; Körner, 2004; Ainsworth & Long, 2005; Körner *et al.*, 2007) has been widely discussed in the literature. CO<sub>2</sub> plays a major role as a limiting resource for carbon assimilation by plants (Farquhar *et al.*, 1980). Several small-scale and open-top chamber experiments have shown an enhancement of photosynthesis in C<sub>3</sub> plants under elevated CO<sub>2</sub> concentrations, leading to increased NPP (Curtis & Wang, 1998; Norby *et al.*, 1999). The long-term effects on real ecosystems, however, are unclear (Norby *et al.*, 1999). Dynamic vegetation models

such as LPJ generally suggest a substantial impact of CO<sub>2</sub> on NPP (Cramer *et al.*, 2001). Measurements from large-scale free-air CO<sub>2</sub> enrichment (FACE) experiments in temperate forests (Norby *et al.*, 2005) have been compared with LPJ model simulations, and showed that the model reproduced the overall response of forest productivity to elevated CO<sub>2</sub> (Hickler *et al.*, 2008). However, these experiments may not be representative of tropical forests. The simulated productivity enhancement in tropical forests was 10% higher than in boreal forests under elevated CO<sub>2</sub>, but supporting data for this response are not available (Hickler *et al.*, 2008).

If the direct impacts of CO<sub>2</sub> on plant productivity and water-use efficiency are great, as assumed in LPJmL and most other global vegetation models (Friedlingstein *et al.*, 2006; Sitch *et al.*, 2008), the dieback risk is almost eliminated. Bayesian weighting of the climate projections shifts the projected biomass changes towards increasing biomass. The consequences for tropical forest ecosystems may be manifold, including faster growth, faster closing canopy gaps, faster reached steady-state leaf area index, and changed successional patterns (Körner, 1998). Different tree species respond differently so that increasing atmospheric CO<sub>2</sub> concentrations in combination with a changing climate may lead to shifts in species composition (Körner, 1998; Raizada *et al.*, 2009).

If direct CO<sub>2</sub> effects are small, the risk of biomass loss remains significant in the Amazon region across most scenarios (c.f. Figs 2 and 3). We investigate the probability of biomass loss and dieback, which we define as an arbitrary limit of biomass reduction of 25% or higher. In a study in southern Amazonia, Alencar *et al.* (2006) shows that this reduction corresponds to the difference in biomass between a tropical forest to a different forest type (ranging from dense to transitional and open forests). A loss of 25% corresponds in our study to a range of 1.5–3.8 kg C m<sup>-2</sup> biomass loss across the five regions. Phillips *et al.* (2009) estimates biomass losses of 0.17–0.80 kg C m<sup>-2</sup> during the 2005 drought in the Amazon region. Equivalent biomass losses of 0.8 kg C m<sup>-2</sup> or more have a 62% probability in eastern Amazonia, a 72% probability in northwestern Amazonia and a 100% probability in southern Amazonia under future conditions assuming no CO<sub>2</sub> fertilization effects. Phillips *et al.* (2009) found that the biomass losses during the 2005 drought were driven by occasional large mortality increases and by widespread but small declines in growth. Mainly light-wooded trees were affected by cavitation or carbon starvation. Brando *et al.* (2008) measured tree mortality and reduction in wood production in a drought experiment in Tapajos, which is located in our eastern Amazonia study region. They observed losses of c. 3.1 kg C m<sup>-2</sup> persisting through their first post-treatment year. Losses were caused mainly by mortality of large trees, and the dead biomass of trees with stem diameter

> 30 cm reached 2.3 kg C m<sup>-2</sup> in the drought treatment plots (Nepstad *et al.*, 2007). According to our results, events similar to this have a low probability in eastern and northwestern Amazonia.

### Range of potential biomass change in five regions of northern South America

The responses of vegetation to climate change in the five large regions of South America investigated can be categorized into three groups: small biomass loss or increasing biomass in eastern and northwest Amazonia, which hold the highest amounts of biomass in dense tropical moist broadleaved forests (as described by Olson *et al.* (2001); Fig. 1) and most of the still intact rainforests. The region has been least affected by land use and hosts the highest amount of biodiversity as a result of stable historical climate conditions (Malhi *et al.*, 2008). Rainforests in northwest Amazonia are highly vulnerable and thus strong efforts should be undertaken to protect this region from deforestation. The uncertainty of biomass change is highest in southern Amazonia. If the actual effects of CO<sub>2</sub> fertilization turn out to be weak, there is a 60% probability for losses of > 25% of the total biomass. The region is covered by highly diverse ecosystems such as the Brazilian savannahs (cerrado) and dry as well as moist tropical forest (Olson *et al.*, 2001). Also in the region of northeastern and southern Brazil the uncertainty is high, but weighting shifts biomass projections towards either no change or an increase in biomass. In contrast to tropical forests in the Amazon basin, the vegetation in this region is adapted to seasonal dry conditions (cf. Fig. 1). These ecosystems are – to a certain extent – less vulnerable to further drying and, in consequence, the projected probability of rainfall reduction (Jupp *et al.*, 2010) does not necessarily lead to biomass loss.

### Conclusions and outlook

We conclude that the risk of Amazon forest dieback is almost eliminated if the direct impacts of CO<sub>2</sub> on plant productivity and water-use efficiency are great. The range of potential biomass change arising from climate model uncertainty remains significant but is, however, smaller than the uncertainty arising from CO<sub>2</sub>-fertilization effects. If direct CO<sub>2</sub> effects are small, the risk of biomass loss is significant in the Amazon region. Thus, CO<sub>2</sub> effects are one of the key unknowns in assessing the risk of Amazonian forest dieback in response to 21st-century climate change. Further research is needed on the differences between the total impacts of climate change caused by CO<sub>2</sub> and other climate-forcing agents on vegetation (e.g. increases in methane or reductions in sulphate aerosols). This has implications for international climate policy, which currently treats all radiative forcings as equally damaging. The risk of Amazon forest dieback

may be many times larger if accelerated climate change arises from agents other than CO<sub>2</sub>.

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## Supporting Information

Additional supporting information may be found in the online version of this article.

**Table S1** Change in temperature ( $\Delta T$ ), precipitation ( $\Delta P$ ) and simulated biomass ( $\Delta B$ ) within the five regions in Amazonia for the period 2070–2100 relative to the baseline (1970–2000) under the climatology of the 24 climate models.

**Table S2** Comparison of plot measurements and simulated grid-cell values.

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